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Allozyme divergence and systematics of Common mole-rats (*Cryptomys*, Bathyergidae, Rodentia) from Zambia

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Abstract

Studied allozymic diversity encoded by 34 gene loci in African common mole-rats, *Cryptomys* sp., comprising two populations from Zambia and re-analyzed allozymic diversity encoded by 25 gene loci in *Cryptomys damarensis, C. hottentotus,* and *C. natalensis* from South Africa. This is the first genetic study of *Cryptomys* populations originating from outside the South African Subregion. The dichotomy between *C. damarensis* on the one hand and *C. hottentotus* and *C. natalensis* on the other hand revealed by previous studies was reconfirmed. Both Zambian populations are specifically distinct from each other and both are distant from all the South African species. Zambian *Cryptomys* are much closer to *C. damarensis* than to both other species. Interpretation of results of the allozymic study is corroborated by data on other biological aspects. We show that currently used morphological criteria for classification of *Cryptomys* are apparently wrong and that the genus *Cryptomys* requires urgently a modern large-scale revision based on allozymes, karyotypes and phenotypic variations.

Introduction

"As a rule, systematic difficulties and doubts arise largely from a paucity of specimens; but *Cryptomys* is a genus which by comparison is already fairly abundantly represented in museums, and every addition so far from making the situation clearer only seems to add to the confusion" (Rosevear 1969, p. 561).

The family Bathyergidae includes subterranean rodents endemic to Africa. It is agreed that the systematic study of this family may elucidate many aspects of evolutionary biology like historical biogeography of Africa, the evolution of eusociality, and the classification and patterns of morphological evolution in rodents (Honeycutt et al. 1991). The family is currently placed into the suborder Hystricognathi, yet even almost fifty years after Simpson's (1945) statement that "Everyone agrees that (bathyergids) are extraordinarily isolated among rodents", a sister-group relationship between the Bathyergidae and any single lineage within the Hystricognathi could not be established (Honeycutt et al. 1991). The family is divided into five genera, the intergeneric relationships being far from clear (see Honeycutt et al. 1991 for the most recent review).

Particularly interesting is the genus *Cryptomys* which, from the standpoint of sociobiology, is considered by some authors as an intermediate link between solitary bathyergids and eusocial naked mole-rats (*Heterocephalus*) (e. g. Jarvis and Bennett 1991; Lovegrove 1991). Unlike other bathyergid genera, *Cryptomys* as a genus is rather eurybiomic (sensu Vrba 1992), occurring from semi-arid to mesic habitats in different soil types over a wide geographical range from Ghana to the Cape (Rosevear 1969). Although it is not a problem to recognize *Cryptomys* as *Cryptomys*, extreme variation in many morphological traits makes taxonomic treatment of this genus very difficult. Thus for instance, 44 and 49 species of *Cryptomys* have been named by Allen (1939) and Ellerman (1940), respec-

tively. This number has been reduced to three species by later authors (cf. Nowak and Paradiso 1983). Most recently, seven species have been recognized by Honeycutt et al. (1991). Different traits like the average size, pelage colouration, white head spots and other markings, shape and size of the infraorbital foramen as well as some other cranial characters have been used for determination and classification by different authors. However, many authors reported significant polymorphism in body size and pelage colouration (which is age and social-dependent in Zambian *Cryptomys*, Burda 1989, 1990), and in white markings even within a single colony. These traits thus cannot be used for species diagnosis if only a small sample is available. Consequently, Rosevear (1969) and Allen (1978) suggested that, in addition to morphological characters, cytology and serology should be brought into account before any reliable taxonomic opinion can be expressed.

Four recent cytologic and genetic studies gave stimuli to revise phylogenetic relationships among bathyergids: Nevo et al. (1986) analyzed karyotype differentiation, Nevo et al. (1987) allozyme differentiation, Honeycutt et al. (1987) mitochondrial DNA restriction-fragment variation, and Honeycutt et al. (1991) mitochondrial nucleotide-sequence variation. With respect to *Cryptomys*, it was demonstrated that two or perhaps even three distinct species, possibly even falling into two genera, can be recognized among the South African forms: *C. damarensis* on the one hand, and *C. (hottentotus) hottentotus* and *C. (hottentotus) natalensis* on the other hand. However, the use of these data for reconstruction of the biogeographic history, evolution of sociality, and intrageneric relationships of *Cryptomys* is limited by the fact that only South African populations were studied, while the genus is much more widely distributed.

We analyzed allozyme diversity in two populations of common (small) *Cryptomys* from Zambia. The present study thus becomes the first genetic investigation of *Cryptomys* from outside the South African Subregion.

Material and methods

Electrophoretic analysis was carried out on 14 specimens of African common mole-rats, *Cryptomys* sp. (Bathyergidae, Rodentia), representing two populations from Zambia, characterized by two different diploid chromosomal numbers (Burda et al. 1992). The karyotype 2 n = 68 originated from Lusaka (locality Chainda in eastern suburbs of Lusaka, vicinity of the University Campus), the animals of the karyotype 2 n = 58 were captured in Itezhi-Tezhi (locality Hot Springs; about 200 km SWW of Lusaka). These two populations were also compared with samples of *C. hottentotus, C. natalensis* and *C. damarensis* from South Africa, involved also in previous analyses by Nevo et al. (1987).

Tissues of each specimen were preserved in the laboratory at −80 °C until processed. Homogenates for electrophoresis were obtained from portions of muscle and kidney tissues crushed in distilled water. Genic variation of structural genes encoding for enzymatic and non-enzymatic proteins was assessed using standard horizontal starch-gel electrophoresis. All gels were prepared using an 11 % suspension of Connaught hydrolyzed starch.

Homogenates obtained from muscle were processed for the following enzymatic proteins: α-Glycerophosphate dehydrogenase (E.C. 1.1.1.8; α-Gpdh), Lactate dehydrogenase (E.C. 1.1.1.27; Ldh-1 and Ldh-2), Malate dehydrogenase (E.C. 1.1.1.37; Mdh-1 and Mdh-2), Malic enzyme (E.C. 1.1.1.40; Me-1 and Me-2), Isocitrate dehydrogenase (E.C. 1.1.1.42; Idh-1 and Idh-2), 6-Phosphogluconate dehydrogenase (E.C. 1.1.1.44; 6-Pgdh), Glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49; G-6-pdh), Indophenol oxidase (E.C. 1.15.1.1; Ipo-1 and Ipo-2), Nucleoside phosphorilase (E.C. 2.4.2.1; Np), Glutamate-oxalacetate transaminase (E.C. 2.6.2.1; Got-1 and Got-2), Hexokinase (E.C. 2.7.1.1; Hk-1), Creatine kinase (E.C. 2.7.3.2; Ck), Adenylate kinase (E.C. 2.7.4.3; Adk), Phosphoglucomutase (E.C. 2.5.7.1; Pgm-1 and Pgm-2), Esterases (E.C. 3.1.1.1; Est-1, Est-2 and Est-3), Acid phosphatase (E.C. 3.1.3.2; Acph), Aminopeptidase (E.C. 3.4.1.1; Ap-1 and Ap-2), Adenosine deaminase (E.C. 3.5.4.4; Ada), Fumarase (E.C. 4.2.1.2; Fum), Mannose phosphate isomerase (E.C. 5.3.1.8; Mpi), and Glucose phosphate isomerase (E.C. 5.3.1.9; Gpi). Homogenates obtained from kidney were processed for the following enzymatic proteins: Alcohol dehydrogenase (E.C. 1.1.1.1; Adh), Sorbitol dehydrogenase (E.C. 1.1.1.14; Sdh), and Xanthine dehydrogenase (E.C. 1.2.3.2.; Xdh).

The employed procedures were described earlier by Nevo et al. (1987) and Filippucci et al. (1988). Isozymes were numbered in order of decreasing mobility from the most anodal one. Allozymes were designated numerically according to their mobility, relative to the most common allele (= 100) (< 100 = slower mobility; > 100 = faster mobility) in *C. (h.) hottentotus* from South Africa.

Allozymic data were analyzed as genotype frequencies with the BIOSYS-1 program of Swofford and Selander (1981). Intrapopulational genetic variation was estimated by the following genetic indices: the mean heterozygosity per locus (observed, Ho, and expected, He), the proportion of polymorphic loci in the population (P 1 %: a locus is considered polymorphic if the frequency of the common allele is not greater than 0.99), and the average number of alleles per locus (A). The amount of genetic divergence between populations was estimated with the indices of standard genetic identity (I) and distance (D) proposed by Nei (1972).

The two populations from Zambia were analyzed for 34 loci. The comparison with the other South African species was carried out on 25 shared loci; the following loci were excluded from this analysis: Shd, Me-2, Ipo-1, Ipo-2, Ck, Adk, Ap-2, Fum, and Est-3.

A dengrogram of the genetic relationships among populations was obtained using the unweighted pair group cluster analysis UPGMA (Sokal and Sneath 1963).

Results

Biological divergence

Some of the relevant intrinsic (morphological, reproductive, sociobiological) as well as extrinsic (ecological) characteristics of Zambian (and South African) *Cryptomys* and their habitats are provided and compared in table 1. Representatives of both populations (Lusaka and Itezhi-Tezhi) possessed eliptical infraorbital foramina (6 skulls of 2n = 68, 3 skulls of 2n = 58 were examined). Two mixed pairs consisting of females of the karyotype 2 n = 68 and males of the 2n = 58 karyotype were kept for seven months. The animals mated normally and regular copulations (observed at least three times a week) were elicited by constant re-pairing of animals (cf. Burda 1989). Both females conceived at least once but resorbed or aborted the embryos within three to four weeks. Even after seven months there was no offspring to any of both females. Subsequent pairing with conspecifics of the same karyotype resulted within few weeks in conception, successfull pregnancy and delivery, and thus confirmed the normal fertility of the involved animals. Further "hybridization" experiments are in progress. They are negative thus far.

Table 1. **Some characteristics of *Cryptomys* and their habitats**

Based on Jarvis and Bennett (1991) and further studies of Bennett and Jarvis cited therein for South African taxa; and on Burda (1989, 1990) for Zambian mole-rats. The given weights refer to mean weights of grown up breeding animals

Species	2n	Weight (g)		Gestation	Eyes open	Colony	Rainfall
		f	m	(days)	(days)	size	(mm/year)
Lusaka	68	75	110	98	24	< 25	840
Itezhi-Tezhi	58	75	110	?(> 70)	?	?(> 12)	> 800
C. damarensis	74, 78	155	200	85	18	< 25	200–600
C. hottentotus	54	65	75	63	13	< 14	200–500
C. natalensis	54	90	105	?	?	?(2–3)	400–600

Pattern of variation

Twenty-three of the thirty-four loci analyzed were monomorphic and fixed for the same allele in the two populations from Zambia: Adh, Sdh, Ldh-1, Ldh-2, Mdh-2, Me-1, Me-2, Idh-1, Idh-2, Ipo-1, Ipo-2, Np, Got-2, Ck, Adk, Pgm-1, Pgm-2, Ap-1, Ap-2, Ada, Fum,

Table 2. **Allelic frequencies observed at the polymorphic and/or discriminant loci for the analyzed populations of the genus *Cryptomys***

Number of examined specimens in parentheses

Loci	Alleles	Lusaka (12)	Itezhi-Tezhi (2)	*C. bott.* (4)	*C. nat.* (4)	*C. dam.* (1)
Adh-1	100	1.00	1.00	1.00	1.00	–
	110	–	–	–	–	1.00
αGpdh	100	–	–	0.87	1.00	–
	103	–	–	–	–	1.00
	104	–	–	0.13	–	–
	106	0.92	0.25	–	–	–
	110	0.08	0.75	–	–	–
Ldh-1	100	1.00	1.00	0.75	1.00	1.00
	105	–	–	0.25	–	–
Mdh-1	100	1.00	0.50	1.00	1.00	1.00
	105	–	0.50	–	–	–
Mdh-2	95	1.00	1.00	–	–	1.00
	100	–	–	1.00	1.00	–
Me-1	98	–	–	–	0.25	–
	100	–	–	0.92	0.75	–
	105	–	–	0.08	–	–
	110	1.00	1.00	–	–	1.00
6Pgdh	90	–	–	–	1.00	–
	95	–	0.25	–	–	–
	100	–	0.75	1.00	–	–
	103	–	–	–	–	1.00
	105	1.00	–	–	–	–
G6pdh	95	0.79	1.00	0.10	0.33	1.00
	100	0.21	–	0.90	0.67	–
Xdh	100	0.85	1.00	1.00	1.00	1.00
	105	0.15	–	–	–	–
Np	100	1.00	1.00	0.83	0.75	0.50
	103	–	–	0.17	0.25	0.50
Got-1	90	0.75	–	–	–	–
	100	0.25	1.00	1.00	1.00	–
	105	–	–	–	–	1.00
Hk-1	100	0.96	1.00	1.00	1.00	1.00
	105	0.04	–	–	–	–
Pgm-2	100	–	–	1.00	1.00	1.00
	103	1.00	1.00	–	–	–
Ap-1	100	–	–	1.00	1.00	–
	108	1.00	1.00	–	–	1.00
Ada	96	–	–	0.08	–	–
	100	–	–	0.92	1.00	–
	105	1.00	1.00	–	–	1.00
Mpi	100	–	–	1.00	1.00	–
	110	1.00	1.00	–	–	1.00
Pgi	90	–	0.75	–	–	–
	96	0.12	–	–	–	–
	100	0.88	0.25	1.00	1.00	1.00

Table 2 (continued)

Loci	Alleles	Lusaka (12)	Itezhi-Tezhi (2)	*C. hott.* (4)	*C. nat.* (4)	*C. dam.* (1)
Acph	100	0.05	–	0.88	1.00	–
	105	0.95	–	0.12	–	1.00
	110	–	1.00	–	–	–
Est-1	100	–	–	0.90	0.88	–
	105	1.00	0.25	–	0.12	1.00
	108	–	0.75	0.10	–	–
Est-2	100	1.00	1.00	0.88	1.00	1.00
	105	–	–	0.12	–	–
Est-3	100	0.88	1.00			
	105	0.12	–			

Mpi, Est-2. The allele frequencies of the polymorphic and/or discriminant loci in the two populations from Zambia and in *C. hottentotus, C. natalensis* and *C. damarensis* from South Africa are given in table 2. For detailed allele frequencies in South African populations see Nevo et al. (1987).

The population from Lusaka (2n = 68) displayed polymorphism at the following loci: αGpdh, G6pdh, Got-1, Hk-1, Pgi, Acph, Xdh, and Est-3.

The population from Itezhi-Tezhi (2n = 58) was polymorphic at the following loci: αGpdh, Mdh-1, 6Pgdh, Pgi, and Est-1.

Genetic summary

The mean value of observed heterozygosity, based on 34 loci, for the populations from Zambia was Ho = 0.052 (Ho = 0.045 in Lusaka and Ho = 0.059 in Itezhi-Tezhi). The mean value of expected heterozygosity was He = 0.066 (He = 0.054 in Lusaka and He = 0.078 in Itezhi-Tezhi). The overall mean proportion of polymorphic loci (P 1 %) for the two populations was P 1 % = 0.191 (P 1 % = 0.253 in Lusaka and P 1 % = 0.147 in Itezhi-Tezhi). The overall mean number of alleles per locus was A = 1.19 (A = 1.24 in Lusaka and A = 1.15 in Itezhi-Tezhi).

Genetic differentiation

Two loci (6Pgdh and Acph) were found discriminant between Lusaka and Itezhi-Tezhi, displaying fixation of alternative alleles. Five loci (αGpdh, Mdh-1, Got-1, Pgi, Est-1) partially discriminated the two populations.

Genetic distance

The values of genetic identity and distance (Nei 1972) between Lusaka and Itezhi-Tezhi populations were I = 0.871 and D = 0.138 respectively.

The values of Nei's genetic identity and distance observed on 25 shared genetic loci between the three South African *Cryptomys* species and both Zambian populations are given in table 3. An UPGMA dendrogram summarizing the genetic relationships found between the populations studied is given in figure 2. In this comparison, the two populations from Zambia displayed a higher value of genetic distance (D = 0.196). The populations from Zambia displayed very high values of genetic distance in comparison with those from South Africa. The values of genetic distance ranged from 0.237 to 0.596. Both populations showed higher affinity with *C. damarensis* (D = 0.300, ranging from

Table 3. **Values of Nei's genetic identity (I; above the diagonal) and distance (D; below the diagonal) between populations of the genus *Cryptomys* from Zambia and South Africa, based on 25 loci**

Population	1 Lusaka	2 Itezhi	3 *C. hott.*	4 *C. nat.*	5 *C. dam.*
1 Lusaka	–	0.822	0.551	0.563	0.789
2 Itzehi-Tezhi	0.196	–	0.571	0.552	0.695
3 *C. hottentot.*	0.596	0.561	–	0.947	0.520
4 *C. natalensis*	0.574	0.594	0.055	–	0.539
5 *C. damarensis*	0.237	0.364	0.654	0.618	–

0.237 in comparison with Lusaka to 0.364 in comparison with Itezhi-Tezhi populations). Equivalent were instead the mean values observed comparing *Cryptomys* from Zambia with *C. hottentotus* (D = 0.578) and *C. natalensis* (D = 0.584).

Discussion

According to Gorman and Renzi (1979), in populations with small sample size (Itezhi-Tezhi), the heterozygosity could change by less than 2.5 % as compared with a larger sample size. The high number of loci analyzed compensates for the small sample size of some populations. Values of heterozygosity and genetic distances are therefore reliable with a reasonable margin of precision (Sarich 1977; Nei 1978; Gorman and Renzi 1979; Sage et al. 1986).

The observed values of genetic variation correspond to the values already observed in South African species of *Cryptomys* by Nevo et al. (1987) and are within the range generally reported for other Rodentia and even that of subterranean rodents which usually display lower genetic variation than above-ground rodents (Nevo et al. 1990).

Our findings on relationships of South African *Cryptomys* corroborate results of previous studies by Honeycutt et al. (1987, 1991) and Nevo et al. (1987) in confirming the dichotomy between *C. damarensis* and *C. hottentotus*, the latter taxon splitting again into two distinct forms: *hottentotus* and *natalensis*.

We suggest that the analyzed Zambian populations comprise two good biological species which are related yet distinct from each other. The distinction is suggested not only by a high value of Nei's D (this study) but also by different karyotypes (Burda et al. 1992), and (if not absolute then for sure relative) postmating reproductive barrier. Whether there is also a premating barrier in nature is not clear. The boundary between both species could not be determined thus far. Using Nei's (1975) criteria (based, however, on presumption of neutrality) (cf. also Nevo et al. 1987), the divergence time ($= 5 \times 10^6 D$) between the two Zambian populations would be about 700 000 (based on 34 loci) to 1 million years (based on 25 loci).

Based on allozymic data, Zambian *Cryptomys* are clearly distinct from all South African taxa. This divergence is confirmed also by different karyotypes (Nevo et al. 1986; Burda et al. 1992) and by (combination of) some biological aspects (e.g. regular age-dependent colour changing in both Zambian *Cryptomys* Burda 1989, 1990, which is absent in *C. damarensis,* Lovegrove pers. comm., and in fact was never noticed in literature dealing with ontogenetic and social development in South African *Cryptomys* – cf. Bennett et al. 1991 and literature cited therein).

Although the examined populations of Zambian *Cryptomys* for sure represent good species, distinct from each other and from the South African taxa, it would be preliminary to describe them formally as new species and to provide them with new specific names.

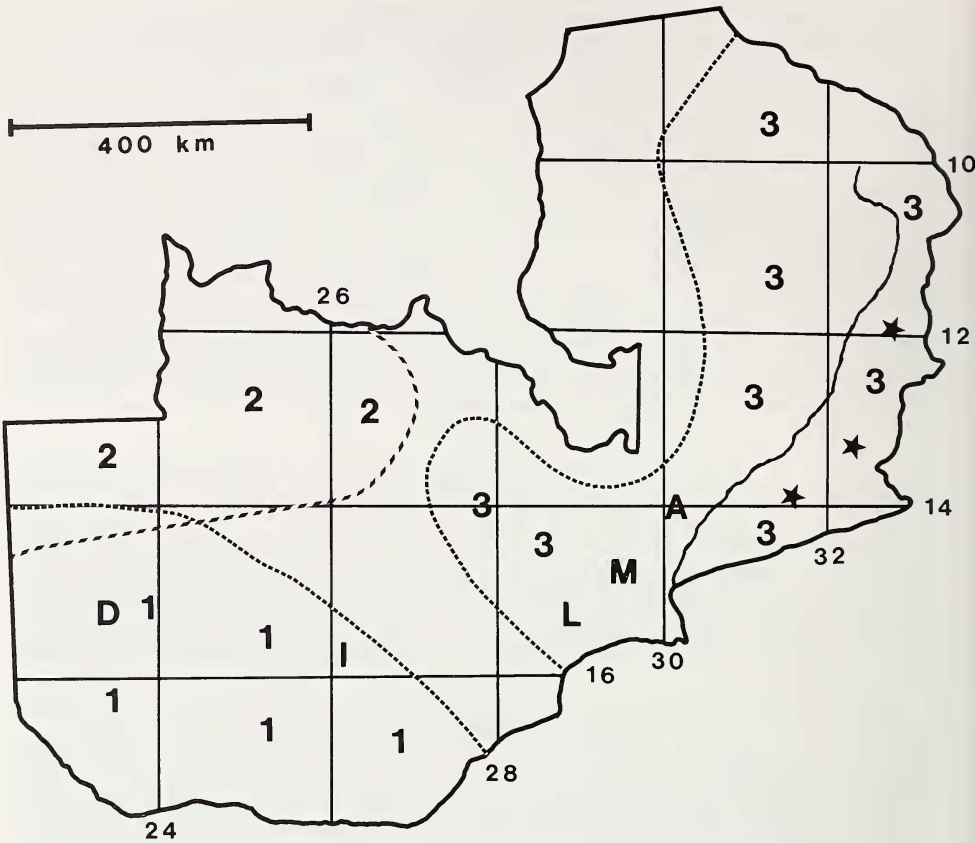

Fig. 1. Map of Zambia. Typical localities of *Cryptomys* taxa described from (what is now) Zambia (according to Allen 1939; Ansell 1978): A = *C. amatus*, D = *C. damarensis micklemi*, M = *C. molyneuxi*. Distribution of different species of common *Cryptomys* across Zambia (according to Honeycutt et al. 1991): 1 = *C. damarensis*, 2 = *C. bocagei*, 3 = *C. hottentotus* (ssp. *amatus*). Note, however, that according to Ansell (1978), no *Cryptomys* occur east of the Luangwa river (asterisk). Localities of *Cryptomys* described in this paper: I = Itezhi Tezhi (2n = 58), L = Lusaka (2n =68)

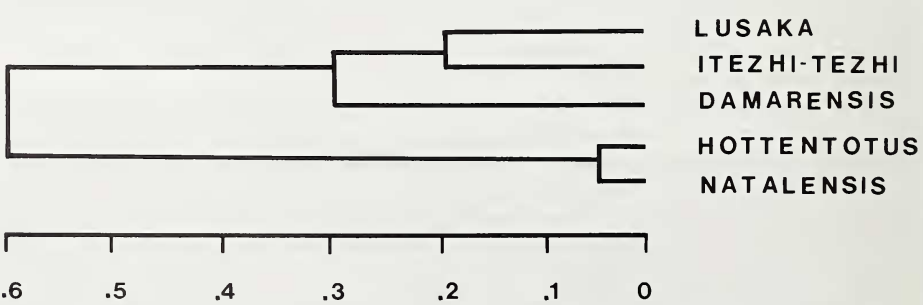

Fig. 2. UPGMA dendrogram summarizing the genetic relationship among populations of the genus *Cryptomys* from Zambia and South Africa, based on 25 loci. The cophenetic coefficient is 0.983

Our restraint is based on the fact that only from (what is now) Zambia, three taxa of common (small) *Cryptomys* were described (cf. Allen 1939): *C. amatus, C. damarensis (micklemi)*, and *C. molyneuxi*. De Graaff (1971), Ansell (1974), Kingdon (1974), and Smithers (1983) considered all Zambian common *Cryptomys* to be only subspecies of a single species, *Cryptomys hottentotus: C. h. hottentotus, C. h. damarensis* (syn. *micklemi*), *C. h. whytei* (syn. *occlussus*), and *C. h. amatus* (syn. *molyneuxi*) (see also Fig. 1). According to Honeycutt et al. (1991), three species of common *Cryptomys: C. hottentotus, C. damarensis,* and *C. bocagei* should occur in Zambia. The Lusaka population should belong to *C. hottentotus amatus,* while the mole-rats from Itezhi-Tezhi should represent *C. damarensis* (cf. Fig. 1). As stated above this was not the case. In order to avoid further nomenclatoric confusion, typical localities must be revisited and topotypical populations must be reexamined by further methods.

In this study we omit giant mole-rats (*Cryptomys mechowi/mellandi*) from Zambia which are for sure distinct from all other *Cryptomys* species (cf. also Burda and Kawalika 1992). The animals which we called *C. hottentotus* in our previous studies belonged to the Lusaka population (2n = 68).

The systematical classification of all *Cryptomys* outside the South African Subregion was based on gross morphological traits only. Honeycutt et al. (1991) divided the seven recognized species into two groups according to the size and shape of the infraorbital foramen. According to the authors, small circular foramina can be found in the central and western African species (including *C. damarensis*) while eliptical foramina are typical of the "*hottentotus*" group inhabiting southern and eastern Africa (incl. Zambia).

In fact, representatives of both populations (Lusaka and Itezhi-Tezhi) possessed eliptical infraorbital foramina. However, Rosevear (1969) (and previous authors quoted by him) and Ansell (1978) reported significant variability in this trait and questioned its usefulness for systematic diagnosis and classification.

In contrast to the classification based on the cranial traits, our genetic findings show higher affinity of Zambian *Cryptomys* to *C. damarensis* rather than to *C. hottentotus*. This relatedness is corroborated also by reproductive (slower pre- and postnatal development) and sociobiological characters (larger families irrespective of diverse climatic and vegetational conditions), and by a more pronounced sexual dimorphism, which are similar in *C. damarensis* and Zambian *Cryptomys* but different from those in *C. hottentotus* (cf. Tab. 1). Apparently, the shape of the infraorbital foramen changed independently and parallelly in diverse lineages. Being most probably neither adaptive nor strictly conservative, this trait thus cannot be employed to elucidate sister relationships in *Cryptomys*.

Even only 200 km apart from each other, in comparable habitas, two distinct *Cryptomys* species were found. Analogously, in Israel across 200 km (however, in different climatic regions), four chromosomal species (considered good biological species) of *Spalax ehrenbergi* occur (e.g. Nevo 1991). We may expect similar speciation in *Cryptomys* range. A large-scale analysis employing karyotypes, allozymes plus other inputs (morphological, physiological, ecological, behavioural, reproductive, natural hybridization etc.) of the genus *Cryptomys* over a broad range of its distribution is needed to provide a definite answer to many interesting questions associated with historical zoogeography, adaptive radiation, and evolution of sociality of *Cryptomys* in particular (and bathyergids and subterranean mammals in general).

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Zusammenfassung

Allozymatische Divergenz und Systematik der Graumulle (Cryptomys, Bathyergidae, Rodentia) aus Sambia

Allozymatische Divergenz (34 Genloci) wurde bei zwei Populationen von afrikanischen Graumullen (*Cryptomys*) aus Sambia untersucht. Diese Untersuchung stellt damit die erste genetische Studie von Graumullpopulationen dar, die von außerhalb der südafrikanischen Region stammen. Zum Vergleich wurden parallel Allozyme (25 Loci) bei *Cryptomys damarensis, C. hottentotus, C. natalensis* aus Südafrika neu analysiert. Eine in früheren Studien schon festgestellte Dichotomie zwischen *C. damarensis* einerseits und *C. hottentotus* und *C. natalensis* andererseits wurde bestätigt. Die zwei untersuchten sambischen Populationen stellen zwei gute biologische Arten dar, die von allen drei südafrikanischen Arten spezifisch unterschieden sind. Sambische *Cryptomys* zeigen eine nähere Verwandtschaftsbeziehung zu *C. damarensis* als zu beiden anderen Arten. Die allozymatischen Befunde und deren Interpretation werden durch den Vergleich mit einigen anderen biologischen Aspekten bestätigt. Es wird gezeigt, daß die morphologischen Kriterien, die zur Zeit für die systematische Bewertung von *Cryptomys* benutzt werden, offensichtlich nicht ausreichend sind und daß eine moderne, breit angelegte Revision der gesamten Gattung notwendig ist.

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